THE CONTROL OF TREE GROWTH BY PHLOEM BLOCKS

Karl Sax

With one plate

The nature of sap movement, nutrient transport and stem polarity in plants has long been known. Thomas Andrew Knight reporting in the Transactions of the Horticultural Society of London in 1822 observed that "the vessels of plants are not equally well calculated to carry their contents in opposite directions" and that "the true sap of trees is wholly generated in the leaves, from which it descends through their bark to the extremities of their roots, depositing in its course the matter which is successively added to the tree." Thus Knight recognized polarity in the transport of elaborated nutrients down the phloem based upon his experiments with inverted cuttings and the effect of girdling the bark of fruit trees. He observed that "it had long been known to gardeners, that taking off a portion of bark round the branch of a fruit-tree occasions the production of much blossom on every part of that branch in the succeeding season." He concluded that the effect of dwarfing stocks in promoting early fruiting and restricting tree growth was similar in nature to the effect of girdling the bark and attributed both effects to the "obstruction of the descending sap."

Phloem blocks induced by killing the stem with steam were used by Dixon (8) and others in their studies on the ascent of sap. The fact that the sap passed up the xylem of the dead stem provided evidence for the "mechanistic" rather than the "vitalistic" theory of the ascent of sap. More recently it has been shown that phloem blocks, induced by killing a section of the stem with heat, prevent the downward movement of vitamins, organic carbohydrates and growth-regulators (Crafts 1951). Bonner (4) girdled the stems of tomato plants with a jet of superheated steam which killed all living tissue. In a few days he found an accumulation of thiamin, pyridoxine, pantothenic acid, riboflavin, sucrose and nitrogen above the girdle. Rabideau and Burr (11) killed sections of bean stems with hot wax and used radioactive carbon to trace the flow of photosynthetic products down the stem. Most of the elaborated organic material accumulated at the dead segment. A phloem block in *Phaseolus* also checked the movement of growth-regulators such as 2,4-D as shown by Weintraub and Brown (15).

It is, however, unnecessary to kill a segment of the stem in order to induce a phloem block. Christensen (5) found that irradiation of a stem segment with X-rays was followed by a swelling of the stem above the irradiated section, and after four or five weeks the swollen area developed roots if the stems were kept moist. The minimum dosage required for such a response was 1500 r for *Xanthium*. Similar results were obtained with *Nicotiana* at 6000 r, *Lycopersicum* at 24,000 r, and *Phaseolus* at 16,000 r, but the minimum dosage required to induce a response was not determined in these genera. The phloem block induced by irradiation checked the flow of organic materials and auxin down the phloem without killing the stem segment.

It is also possible to impose a phloem block without killing the stem by inverting the scion or by inverting a ring of bark. This technique is based upon the polarity of phloem transport. The botanical studies of stem polarity date back to the work of Vöctung and Sachs with their description of "root-pole" and "shoot-pole." The role of polarity in grafting was probably known by horticulturists for hundreds of years. It was described by the botanist Strasburger (14) as follows — "Unlike poles of a plant may readily be induced to grow together, while like poles may only be brought to do so with difficulty and then do not develop vigorously." This conclusion has been confirmed repeatedly. The inversion of the rootstock has, however, been used to stimulate rooting at the base of the scion in order to get varieties of apple trees on their own roots. Kerr (10) found that such an inverted graft would survive long enough to permit scion rooting above the graft union, due presumably to the accumulation of auxin at the junction of the "root-poles" of stock and scion.

The induction of a phloem block by inverting a ring of bark was reported in 1935, but it is probable that it was also used by the early horticulturists of Europe. According to Roberts (12) the inverted rings checked the growth of the tree, but without the deleterious effect resulting from girdling. Apparently this work was not continued by Roberts.

It is also known that certain incompatible combinations of stock and scion check tree growth as a result of a phloem block induced by an imperfect graft union (2). In some cases, however, the graft union appears to be normal yet there is considerable overgrowth of the scion accompanied by dwarfed growth and precocious fruiting. In these cases perhaps the stem of the scion can utilize the organic carbohydrates from its leaves more effectively than can the stem of the rootstock.

There is some evidence that the dwarfing effect of certain Malling apple rootstocks may be due to a retardation of phloem transport. Dr. F. R. Tubbs, Director of the East Malling Research Station, writes that: "We do not know of any dwarfing apple rootstock that does not induce the formation of a bulge" (personal communication). This swelling of the stem of the rootstock or the section of the interstock could be attributed to the retardation of the downward flow of elaborated organic nutrients and growth stimulants, as suggested by Knight, thus promoting more rapid growth of the Malling rootstock or interstock stem. The fact that a long dwarfing interstock is more effective than a short one, and that certain rootstocks are more dwarfing if budded high on the stem than if budded near the ground, would seem to support the above interpretation (13).

It is known that the dwarfing effects of certain rootstocks are due to factors other than the blocking or retardation of phloem transport. Colby (6) has suggested that the extreme dwarfing effect of the Malling IX apple rootstock may be due to early suberization of the young roots. There is also evidence that growth can be suppressed, quite independently of the nature of the graft union, by an interaction between the scion variety and the root system of the stock (Sax, Proc. Am. Soc. Hort. Sci., in press).

During the past five years a study of the effect of inverting rings of bark has provided some information on the mechanism of phloem transport and has provided another method for dwarfing fruit and ornamental trees. We began with the inversion of a single ring of bark about an inch long on the stems of one- and two-year-old apple trees. The cuts through the bark were made as parallel as possible, sometimes by using a double bladed knife — in other cases by using a strip of metal tape as a guide. The bark was removed, inverted and wrapped tightly with a rubber band, until the bark had healed onto the stem — a period of a week or ten days.

The inverted bark made little or no growth, but there was a swelling of the stem above the inverted bark and to a lesser extent at the upper edge of the inverted section of bark. At the vertical seam of the inverted ring there was regeneration of tissue and after several months this area had made considerable growth, and after several years it had so dominated the inverted area that the dwarfing effect was largely lost. Apparently there is normal polarity of phloem transport in this regenerated area and it grows rapidly.

In order to effect a more permanent phloem block it was necessary to invert two rings of bark, one directly above the other, and orient the vertical seams on opposite sides of the stem. There is some phloem regeneration at the seams, but any downward transport through the seam of the upper inverted ring is checked when it reaches the intact edge of the lower inverted ring with its vertical seam on the opposite side. A Cortland apple whip was treated in this way five years ago. It has made almost no growth in trunk diameter and has increased in height only about six inches during the past five years, but it has borne several fruits during each of the past two years and appears to be healthy.

In 1953, a group of Baldwin apple trees, budded on a semi-dwarfing rootstock, were used for a bark inversion test. A single ring of bark was inverted on eight two-year-old trees, and above the vertical seam a square of bark was inverted to prevent transport down the regenerated tissue. In the eight controls a ring of bark was removed and replaced in the normal position. In both the bark inversion series and in the controls there was some early sucker growth below the rings, and the first growth of suckers were removed. Subsequent sucker growth was limited almost entirely to the trees with inverted bark. At the end of the growing season the trunk diameter below the bark ring was measured, together with tree height and total length of the branches developed below the inverted bark rings. The results are shown in Table 1, and photographs of a control and of an inverted bark tree are shown in Figures 1 and 2.

The data show that the inversion of the ring of bark reduced the growth of the trees both in trunk diameter and in height. It also promoted the growth of buds below the phloem block, indicating that the auxins which normally suppress bud development at the base of the trunk had not passed through the inverted ring of bark in sufficient quantities to suppress bud growth. Most of the trees with the inverted bark have flower buds while no flower buds were observed on the control trees. The inverted bark remains alive, so far as can be determined by its appearance, yet growth is suppressed and earlier fruiting is induced.

TABLE 1.

EFFECT OF BARK INVERSION ON TREE GROWTH
Baldwin/524/sikkimensis.
Bark inverted June 1, '53. Measured Oct. 6, '53.

8 Controls			8 Inverted		
Trunk Caliper cm.	Height Feet	Sucker Growth ft.	Trunk Caliper cm.	Height Feet	Sucker Growth ft.
2.0	4.5	0	1.5	3.8	4.1
1.7	5.1	0	1.1	3.1	4.2
1.9	4.6	0	1.4	3.2	4.5
2.1	4.9	0	1.4	3.2	5.1
1.9	4.5	0	1.4	3.1	4.9
1.9	4.0	0	1.6	3.5	2.1
1.6	4.2	0.5	1.5	3.5	3.2
2.1	4.1	0	1.5	3.6	4.7
Ave. 1.9	4.5	−0.1	1.4	3.4	4.1

It should be possible to modify the bark inversion phloem block to permit the desired amount of growth of the tree. A method developed several years ago appears to meet this need. Baldwin two-year-old trees, budded on *Malus sikkimensis* rootstocks, were used. Two bark inversions were made with eight-inch strips of normal bark on opposite sides of the trunk, and the inverted rings were separated by a short segment of normal bark of half an inch to one inch in length. The downward movement through the phloem was limited to the slender strip of normally oriented bark. After passing down the first ring the flow must pass laterally before it can pass down the normal strip of bark in the second ring. Although lateral phloem transport is restricted some material does get through as is evident from the growth shown in Figure 4. It is probable that a short section of normal bark between the inverted rings would have a greater restriction on phloem transport than a long one, so that the degree of dwarfing could be regulated to some extent by varying the length of the central segment between the inverted rings. Thus by adjusting the width of the normal strips of bark in the inverted rings and by varying the length of the normal central segment, it should be possible to obtain any desired degree of dwarfing.

All of these treated trees flowered and several bore fruit the following year. One of these trees, bearing abundant flower buds as it begins its fourth season's growth, is shown in Figure 3. The details of the double bark inversion are shown in Figure 4. The growth of the normally polarized strips of bark in the inverted rings may eventually result in a direct line of phloem transport through the normal ring of bark between the inverted segments, and the dwarfing effect will be reduced and finally lost. In order to maintain a permanent dwarfing effect the inverted bark technique may have to be repeated, but when a tree reaches the desired size a double inversion with only a very narrow ring of bark (or none at all) between the inverted rings, should insure permanent dwarfing. Since the bark inversion may have to be repeated, this technique for dwarfing trees is not likely to be of much value to the commercial nurseryman. The average back yard horticulturist should, however, have no trouble in using this technique.

In a few cases we have put double upside-down adjacent rings on larger trees (up to 6 inches in diameter) with the hope that further growth could be checked almost completely and yet permit flowering and fruiting. These trees have been treated only for one growing season, and at least several years must elapse before we can recommend such a procedure.

The inactivation of the phloem by ionizing radiation is comparable in several respects to the effects of inverting a ring of bark. The phloem block is induced without killing the bark, swelling of the stem occurs above the treated area and bud growth is stimulated below the phloem block just as it is by inverting the bark. On July 27 the stems of a clonal line of young poplar trees were irradiated with 2,500, 5,000 and 10,000 roentgen units of X-rays respectively. A lead plate with a 1.5 inch slit was placed over the stems to limit the radiation to the short stem segment. After several weeks the swelling above the irradiated areas became evident particularly at the higher doses. On Oct. 6th the six trees receiving 2500 or 5000 r were all alive, but at 10,000 r four of five treated trees were dead above, at, and for some distance below the irradiated segment. This higher dosage may have killed the tissue completely, followed by the separation of the bark from the xylem as a result of the overgrowth of the stem above the irradiated area, as shown in Figure 3. The inverted bark produced a similar overgrowth, but without pulling the bark from the stem in the treated segment. At the lower doses of X-rays there was evidence of a phloem block with no death of the stem at the irradiated area.

It is evident that it is possible to produce a phloem block without killing the stem by inverting a ring of bark or by non-lethal exposure of a stem segment to X-rays. In both cases the growth of the treated area is restricted or suppressed. The suppression of growth may be the cause of the phloem block in these cases. According to Abbe and Crafts (1) —"It is characteristic of the sieve tubes of all plants, that, after a brief functioning period — consisting of from a few days in the case of protophloem sieve tubes to a single season in most woody plants — the elements collapse, and death occurs."

The X-ray induction of a phloem block without killing the tissue is apparently due to nuclear injury which prevents continued cell division without killing the cytoplasm. It is known that the cytoplasm is very much more resistant to injury from X-rays than is the nucleus. Thus the sieve tubes already formed could continue to function, but no new ones would be formed to augment and replace those present at the time of irradiation.

The bark inversion also seems to produce a phloem block by the inhibition of cell division. The suppression of growth in the inverted bark rings is apparently due to the inability of nutrients and auxins to move freely against the reversed polarity. There is usually a slight swelling of the top of the inverted bark ring, indicating some diffusion of nutrients, but there is little or no growth of the inverted segment as a whole. Thus the inversion of the bark may check growth by the failure of nutrients to move freely through the inverted phloem tissue.

The new phloem produced at the vertical seam in inverted bark segments appears to be normally polarized since this tissue grows rapidly. Any new phloem tissue produced within the inverted ring of bark should eventually also be normally polarized, but the fact that growth does not occur indicates that few or no sieve tubes are produced, presumably due to the checking of nutrient flow through the inverted segment. The fact that bark inversions made early in the growing season do not survive as well as those made in June and August suggests that some active sieve tubes are needed even though the inverted polarity checks the passage of nutrients and auxins down the stem. Since a tree has lived for five years with a double inverted ring of bark, some material must be transmitted either through the inverted bark or through some other part of the stem.

SUMMARY

A phloem block can be induced without killing the stem tissues by exposing stem segments to X-rays sufficient to suppress cell division or by inverting a ring of bark. The phloem block induced by irradiation appears to be due to the failure of renewal of phloem elements. The reversed polarity of the inverted ring of bark also prevents renewal of phloem elements, presumably by preventing the adequate movement of nutrients and auxins into the inverted phloem cells. The inversion of rings of bark may be modified to produce the degree of dwarfing desired in fruit and ornamental trees.

BUSSEY INSTITUTION AND ARNOLD ARBORETUM,
HARVARD UNIVERSITY

LITERATURE CITED

1. Abbe, Lucy B. and Crafts, A. S. Phloem of white pine and other coniferous species. Bot. Gaz. **100**: 695–722. 1939.
2. Argles, G. K. Stock-scion incompatibility in fruit trees. Imp. Bur. Fruit Production. East Malling, Kent, England. 1937.
3. Biddulph, O. and Marple, J. Translocation of radiophosphorus in the phloem of the cotton plant. Amer. Jour. Bot. **31**: 65–70. 1944.
4. Bonner, James. Accumulation of various substances in girdled stem of tomato plants. Amer. Jour. Bot. **31**: 551–555. 1944.
5. Christensen, Eric. Root production in plants following localized stem irradiation. Science **119**: 127–128. 1954.
6. Colby, H. L. Stock-scion chemistry and the fruiting relationships in apple trees. Plant Physiol. **10**: 483–98. 1935.
7. Crafts, A. S. Movement of assimilates, viruses, growth regulators, and chemical indicators in plants. Bot. Rev. **17**: 203–284. 1951.
8. Dixon, H. H. Transpiration and the ascent of sap in plants. Macmillan & Co. Ltd. London. 1914.
9. Esau, Katherine. Development and structure of phloem tissue. Bot. Rev. **16**: 67–114. 1950.
10. Kerr, W. L. A simple method of obtaining fruit trees on their own roots. Proc. Amer. Soc. Hort. Sci. **33**: 355–357. 1935.
11. Rabideau, G. S. and Burr, G. O. The use of C^{13} isotope as a tracer for transport studies in plants. Amer. Jour. Bot. **32**: 349–356. 1945.
12. Roberts, R. H. A further trial of ring grafting to produce stock effects. Proc. Amer. Soc. Hort. Sci. **33**: 358–359. 1935.
13. Roberts, R. H. Theoretical aspects of graftage. Bot. Rev. **15**: 423–463. 1949.
14. Strasburger, E. et al. A Textbook of Botany. Macmillan and Co. Ltd. London. 1898.
15. Weintraub, R. L. and Brown, J. W. Translocation of exogenous growth-regulators in the bean seedling. Plant Physiol. **25**: 140–149. 1950.

DESCRIPTION OF FIGURES

FIG. 1. Baldwin tree, 2 years old, on semi-dwarfing rootstock. A ring of bark was removed and replaced in the normal position on June 1, 1953. This control tree has made considerable growth in a single season.

FIG. 2. Baldwin tree, 2 years old, on semi-dwarfing rootstock. A ring of bark was inverted June 1, 1953. Note dwarfing effect in a single season, and the production of flower buds. The suckering below the inverted ring of bark indicates the checking of auxin flow.

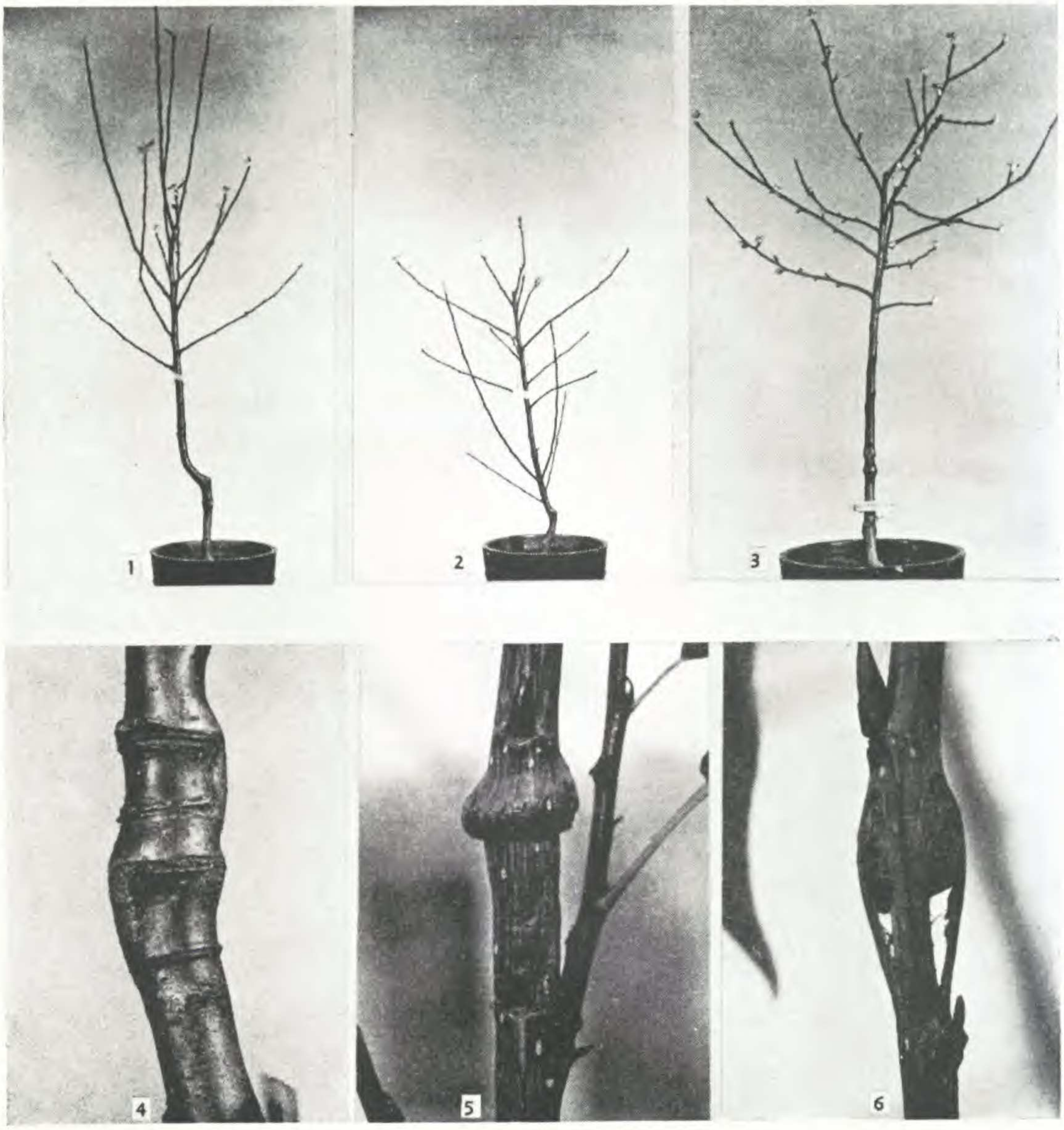
FIG. 3. Baldwin on *M. sikkimensis*, 3 years old, dwarfed by double inverted ring with a slender strip of normal bark on the opposite side of each of the two inverted rings. A short section of normal bark was left between the two inverted rings. This tree bore fruit in its third growing season and bears many flower buds as it begins its fourth year.

FIG. 4. Details of double bark inversion show how phloem transport is checked. The swelling of the upper end of the inverted ring of bark suggests some nutrients and auxins may flow into the inverted bark by diffusion, but active phloem transport is blocked by the reversed polarity of the inverted phloem tissue.

FIG. 5. A poplar stem with inverted ring of bark, showing swelling of the stem above the phloem block imposed by reversed polarity of the phloem.

FIG. 6. A poplar stem exposed to 10,000 r of X-rays. Note the similar swelling of the stem above, and the suckering below, of the irradiated section of stem. The X-rays impose a phloem block by preventing cell division and the renewal of phloem cells. In this case the bark was killed and is pulled away from the wood by the expansion of the stem above the irradiated area, but it is possible to impose a phloem block with X-rays without killing the tissue.

Photographs by Heman Howard.



Control of Tree Growth by Phloem Blocks